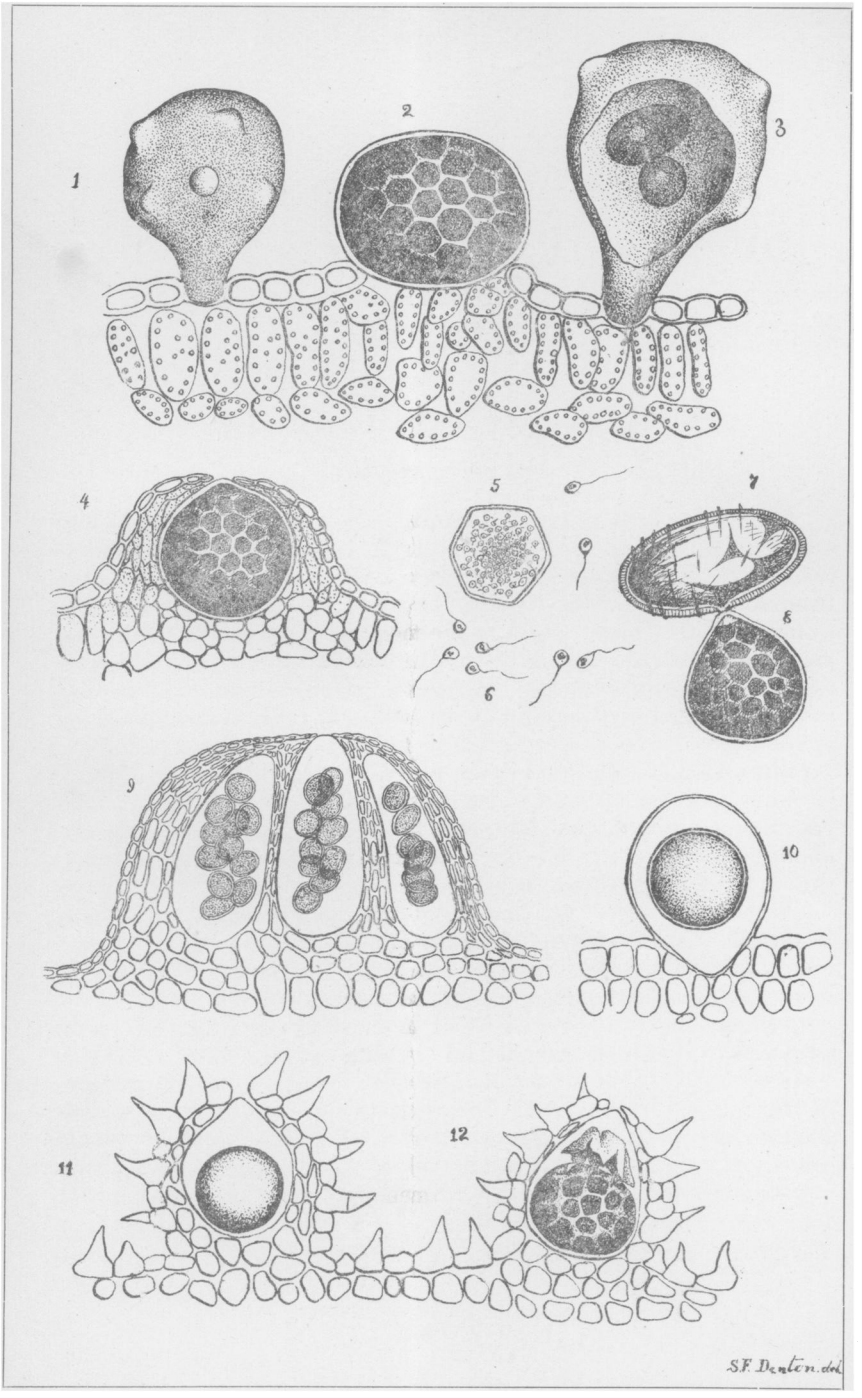

FARLOW ON SYNCHYTRIA.

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The Synchytria of the United States.

BY W. G. FARLOW.

The genus *Synchytrium* includes a number of species which are parasitic in the epidermal cells of land plants, and produce deformities not unlike the galls caused by the attacks of some insects. In a previous paper[1] I gave an account of the species known in this country, and since then I have received additional material from different parts of the United States. As it is necessary, in order to obtain a satisfactory knowledge of the species, to study their development as well as their morphological characters, I have, in the present paper, given an account of the species which are known to me in the United States, hoping that, to the information which I have obtained principally from dried specimens, others who live in the regions where the species abound may, hereafter, add observations on the development of the imperfectly known forms.

Our first exact knowledge of the genus *Synchytrium* dates from the classic paper of de Bary and Woronin on the Development of the *Chytridiaceæ*[2], and since then Woronin[3] and Schroeter[4] have published important papers on the subject.

Before describing our species in detail, I shall give a short account of the development and structure of *Synchytria*, but it is impossible, in this connection, to refer to the systematic position of the genus further than to say that it belongs to the *Chytridiaceæ*, an order including a number of genera, most of which are colorless parasites in aquatic plants, and differ from *Synchytrium* in generally having a rudimentary mycelium or rhizoidal

[1] Bulletin of the Bussey Institution, ii. p. 229.
[2] Bericht Naturforsch. Gesell. Freiburg, 1863.
[3] Bot. Zeitung, xxvi.
[4] Beitr. zur Biologie, ii, part 1.

apparatus connected with the reproductive cells, while in *Synchytrium* there is no trace of mycelium. For an account of the relations of this group of parasites to other fungi the reader should consult de Bary's[1] recent work.

The parasite while in its zoosporic stage makes its way into an epidermal cell, which then increases rapidly in size. In the simplest cases, as *S. papillatum* and *S. Myosotidis*, the cells grow out beyond the surface of the leaves in the form of more or less spherical sacks, which look to the naked eye like small glands. In other cases the epidermal cells do not rise above the surface, but protrude inwards into the leaf. More frequently, however, the epidermal cells swell and push outwards, and at the same time the neighboring cells increase in number, so that a protuberance or gall is formed on the leaves. The shape and general appearance of the galls vary with the different species, and are, as a rule, characteristic. When the galls are abundant the leaves or stems on which they are borne are frequently curled or knotted. There is usually a discoloration, which is not unfrequently striking. This is sometimes due to the presence of a colored fluid in the cells which are attacked by the parasite, and which may be called *host-cells;* but, more frequently, it is in the adjoining cells.

Once inside its host-cell the parasite increases in size and develops into a spherical or elliptical cell, which as it matures becomes either a resting spore or a sorus In the simplest cases, as *S. Anemones*, the cell wall thickens, and is composed of two coats, an epispore and an endospore, the former being dark, thick and brittle, and the latter thin and lighter colored. Generally only one resting spore is found in a single host-cell, but it sometimes happens that the cells are attacked by more than one parasite, and then we may have several resting spores in a cell. In extreme cases, as *S. pluriannulatum*, there are as many as 25, or even more, resting spores in a cell. The resting spores are produced principally towards the end of the season, and are set free by the rotting away of the leaves in which they are contained. In species like *S. papillatum*, where the host-cells form bladders on the surface of the leaves, the cells are brittle and readily break off, and in this way the resting spores escape.

The spores germinate in one of two ways. In the first the epispore cracks open and the endospore and its contents exude

[1]Vergleichende Morphologie und Biologie der Pilze, Mycetozoen and Bacterien.

and form a sphere, which is attached at one point to the remains of the epispore. The contents of the sphere then divide so as to form a number of closely packed cells, the *zoosporangia*. The whole mass of zoosporangia constitutes a *sorus*. The zoosporangia soon separate from one another, and, when free, they are at first irregularly polyedral, but become afterwards more or less spherical. The contents of each zoosporangium then separate into a large number of zoospores, which escape by a rupture of the wall of the zoosporangium The individual zoospores have, in general, a circular form with a bright orange spot in the interior and a single cilium, or, in exceptional cases, two cilia. The zoospores, after swimming about for an indefinite period, attach themselves to the epidermal cells of some host plant and again develop into resting spores. In the second mode of germination the endospore and its contents do not protrude in the form of a bladder, but are transformed into zoosporangia while within the epispore.

A considerable number of the species of *Synchytrium* develop in the manner described above; that is, briefly, from the zoospores arising from the germination of the resting spores in spring, new resting spores are produced in the host cells. The species which develop in this way are placed by de Bary in the subgenus *Pycnochytrium*. In the subgenus *Eusynchytrium* the development is more complicated. The resting spores germinate as before, but after the zoospores have made their way into a host-cell they do not at once form new resting spores, but develop into what have been called summer sori, and in the specific descriptions which follow this is what is referred to under the term sorus, and not the sori formed directly in the germination of the resting spores. In *Eusynchytrium* the zoospores make their way into the epidermal cells and grow into large cells which generally almost completely fill the host-cells. These large cells are sori, and the contents form at once zoosporangia, whose appearance and subsequent development are the same as in *Pycnochytrium*. This formation of summer sori may be repeated several times during the season, but ultimately the zoospores produce resting spores at the end of the season. In a few of the species of *Eusynchytrium*, the summer sorus does not fill the host cell, but, when mature, the wall of the sorus ruptures within the host-cell and the mass of zoosporangia is set free in the host-cell, the wall of the sorus remaining behind as a shrivelled membrane.

Those who wish to study the formation of the sori and zoospores will find excellent material in the species which forms bright

yellow spots looking like a uredo on *Amphicarpœa monoica*. The leaves may be gathered and placed in a moist place, or dipped into water on glass slides or in watch-glasses. In a few hours the water will be colored orange from the abundance of escaped zoosporangia and zoospores. All the stages of development may easily be seen, and healthy leaves may be infected by leaving them a short time in the water and then removing them and keeping them in a moist place for a few days. One who wishes to experiment on the motions of chlorophyl-free zoospores can obtain an abundance of zoospores by placing a few infected leaves of *Amphicarpœa* in glasses of water.

From an economical point of view the *Synchytria* are not of great importance. None of our species attack important agricultural or ornamental plants. These parasites do not spread with great rapidity, and as they do not grow through the hosts which they inhabit but only attack them in superficial spots, they are not very destructive. Unlike many other fungi which attack living plants, the *Synchytria* are supposed not to be limited to one species of host, or to species nearly related botanically, but the same *Synchytrium* may inhabit plants belonging to different orders. The species of *Synchytrium* are distinguished by the presence or absence of summer sori, the nature of the galls or deformities produced, and the shape and size of the resting spores, and it may be asked how far these points might be modified by the host plant in case of species which are said to inhabit several different hosts. A study of the development and cultures are necessary in order to settle the limits of the species accurately.

The following account includes all the species known to me in the United States. The synonyms are given with references to American works where the species are mentioned, an also the original European references. Of the species not yet known in this country we might expect to find *S. Taraxaci*, D.By. and Wor., *S Stellariæ*, Fuckel, and *S. globosum*, Schrt. on *Viola*.

SYNCHYTRIUM D.By. & Wor

Unicellular fungi inhabiting the epidermal cells of living plants, entirely destitute of mycelium. Reproduction by resting spores and sori containing zoosporangia from which are produced zoospores having one, or rarely two, cilia. Conjugation wanting.

A. EUSYNCHYTRIUM. Resting spores and summer sori both present[1].

[1] In *S. decipiens*, here placed on account of its apparently close relation to *S. Taraxaci* and *S. fulgens*, no resting spores have yet been found.

1. S. PAPILLATUM Farlow.

Bull. Bussey Inst. ii, p. 233.
Catalogue Pacific Fungi, p. 25.
Ellis N. Am. Fungi no. 202.

Spots dark purple, galls glandular, formed of papillate, pyriformly swollen epidermal cells, resting spores elliptical, .06–.07 mm. by .04–.05mm., epispore brown, somewhat roughened. Sori superficial, spherical, .10–.12mm. in diameter.

On leaves of *Erodium cicutarium*, L'Her.

California.

The distortions produced by this species are confined to the epidermal cells, which swell into large pyriform sacks, whose surface is raised in large, conical, scattered papillæ. To the naked eye the swollen cells look like purple glands, which are often so abundant as to nearly cover the surface of the leaves, and remind one of the so-called species of *Erineum*. Each cell contains from one to three resting spores which are small in comparison with the host-cell, while the contrary is true in *S. Myosotidis*, in which the galls are somewhat similar to those of the present species. The sori in the specimens examined were much less abundant than the resting spores, and were formed in epidermal cells which became more or less spherical and projected above the surface of the leaf. The species is known only in California, although *Erodium cicutarium* is a common European weed, and occurs somewhat rarely as an introduced plant in our Atlantic States. If the *Synchytrium* is really, as it seems to be, an endemic species in California, one would expect to find it on some other host than the *Erodium*, which is an introduced plant. The species is easily recognized, and may very likely be found hereafter on other hosts.

2. S. HOLWAYI Farlow.

Spots purple, galls hemispherical or subglobose, resting spores spherical, 07–.09mm. in diameter, epispore smooth, dark brown. Sori spherical, .09–.10mm. in diameter, maturing in the host cell.

On leaves of *Monarda*.

Decorah, Iowa.

This is another of the interesting forms found by Mr. Holway, who states that the parasite is common near Decorah. The affected leaves assume a dingy purple color, and the galls are abundant, especially on the bases of the leaves and petioles. Sections show that the galls are formed of large host-cells surrounded by the leaf-cells, the whole forming a hemispherical, or frequently almost a spherical, protuberance on the surface of the leaves. Some of the host-cells contain resting spores which are generally solitary. Other host-cells contain the sori, which are yellow colored spheres resting on the bottom of the host-cells. The wall of the sorus ruptures before it has escaped from the host-cell and the zoosporangia remain in a mass at the base of the host-cell, while the shrivelled wall of the sorus remains at the apex of the cell, as in *S. Stellariæ* Fuckel figured by Schroeter.

As far as the galls and resting spores are concerned the present species might be considered a form of *S. aureum*, which is said by Schroeter to occur on *Prunella vulgaris* in Europe; but in *S. aureum* sori have never been found, so far as I know, while in our form they are common, and, as has already been said, like those of *S. Stellariæ*, a species abundantly different from ours in the resting spores and deformities produced. *S. Holwayi* may then be considered distinct, at least until it shall hereafter be discovered that *S. aureum* has similar sori.

3. S. FULGENS Schroeter.

Hedwigia, xii, p. 141 and Fung. Eur. no. 1656.
Catalogue Pacific Fungi, p. 25.

Spots minute, purple, resting spores spherical, .066–.082mm. in diameter, epispore dark brown, smooth. Sori spherical or elliptical, .06–.10mm. in diameter, bright yellow.

On *Œnothera biennis*, L.

California. Europe.

This species is reported by Harkness and Moore in California in their Catalogue l. c. It is to be expected in the Eastern States, but I have never been able to detect it near Cambridge. It is also said to occur in Illinois. The description given above is taken from Schroeter.

4. S. INNOMINATUM.

Spots dark red, resting spores globose or slightly elliptical, .07–.10mm.in diameter, epispore thin and smooth, in oval host-cells which do not project beyond the surface of the leaves Sori yellow, about .12–.15mm. in diameter, sunk in the leaves.

On leaves of *Malacothrix*.

Santa Cruz, Cal.

The present form was found by Dr. C. L. Anderson on leaves of *Malacothrix*. When the parasite is not very abundant the leaves are turned dark red, but not distorted. When it is abundant, however, the leaves are reduced in size and become irregularly knotted and twisted. The affected cells swell to a considerable size, but are always sunk in the leaves and do not rise above the surface, so as to form galls properly speaking. The resting spores are found one or two in a cell. The sori, unlike those of *S. Holwayi*, completely fill the host-cell when mature. The species is certainly closely related to *S. Taraxaci*, D. By. & Wor., and it may be the *S. sanguineum* Schroeter, said in Bericht. Schlesisch. Gesell. 1875, to be nearly related to *S. Taraxaci*, but of which I have seen no description. I have thought best to avoid giving a name to our form until it shall be proved, on further examination, to be clearly distinct from the two species just mentioned.

5. S. DECIPIENS.

Uredo Leguminosarum and *U. Fabæ* in Herb. Curtis.
Uredo æcidioides Peck in 24th Report New York State Museum, p. 88.
Uredo Peckii Thuemen, Mycologia Universalis no. 538; Peck 29th Rept. p. 75.
Synchytrium fulgens var. *decipiens* Farlow, Bull. Bussey Inst. ii, p. 229; Ellis N. Am. Fungi no. 201; Trans. Wisconsin Acad. i, p. 4.

Spots bright yellow, galls hemispherical, sori spherical, .18–.20 mm. in diameter, zoosporangia about .015mm. in diameter, generally very numerous. Resting spores unknown.

On leaves and stems of *Amphicarpæa monoica*, Nutt.

Massachusetts to Minnesota and southward to Maryland.

The most common and striking species in the Northern States, but the southern limit is not sufficiently known. In Bull. Bussey Inst. l. c. I gave a detailed account of the development of the sori and their germination, but common as the species is I have never found resting spores. The species abounds near Cambridge from the middle of May until the middle of October. The young plants, as soon as they can be recognized in the spring, are often covered with the bright yellow sori, which are frequently mistaken for a uredo. After the sporangia have been discharged the spots resemble æcidia. I can find no difference later in the season, and when vegetation is killed by the frost in October the sori are as abundant as ever, but no trace of resting spores has been found. Surely, if our plant bears resting spores which resemble those of *S. fulgens*, there ought to be no difficulty in detecting them. As it is, it seems to me best to consider our form as distinct from *S. fulgens*, of which I formerly considered it a variety, relying on the resemblance of the sori which, in both cases, are bright yellow, and project rather prominently at first, but afterwards assume an æcidium-like form.

B. PYCNOCHYTRIUM. Resting spores present, but summer sori wanting.

6. S. ANEMONES Wor.

Bot Zeit. xxvi, Pl. 3, f. 31–36.
Bull. Bussey Inst. ii, 224, 229.
Trans. Wisconsin Acad. vi, 4.
Ellis N. Am. Fung. no. 203.

Spots minute, dark violet, galls hemispherical, resting spores solitary, or sometimes two in a cell, spherical or slightly elliptical, about .08–.12mm. in length, epispore dark brown, somewhat rough.

On leaves and petioles of *Anemone nemorosa*, L.

Massachusetts to Wisconsin. Europe.

Probably common wherever the *Anemone* is found. Usually in company with other fungi, but easily recognized by the minute dark-violet spots which are generally scattered, but sometimes densely crowded, especially on the lower parts of the leaves and petioles.

7. S. ANOMALUM Schroeter.

Beit. zur Biologie i, part 1, 40, Pl. 1, f. 5-7.

Spots minute, pale yellow becoming darker, galls flattened hemispherical, resting spores elliptical, about .12–.20mm. by .09–.12mm., epispore dark brown, smooth.

On leaves and petioles of *Adoxa Moschatellina*, L.

Decorah, Iowa. Europe.

The only American specimens which I have received were collected by Mr. E. W. Holway. The fungus is, I think, without doubt the same as that described by Schroeter. Mr. Holway's specimens, however, showed great uniformity in the size and shape of the spores, which were distinctly elliptical, whereas Schroeter describes them as very variable. The galls differ from those of the last named species in that the host-cell enlarges so as to occupy a great part of the thickness of the leaf, but does not project much above the surface and is there only loosely covered by the neighboring cells. Occasionally the parasite develops in a subepidermal cell, in which case there is but little swelling of the leaf.

8. S. AUREUM Schroeter.

Beit. zur Biol. i, part 1, p. 40, Pl. 3, f. 8–12.

Spots golden yellow often bordered with red, galls hemispherical, resting spores spherical, about .10–.20mm., epispore brown, smooth.

On leaves and stalks of *Lysimachia quadrifolia*, L.

Granville, Mass. Europe.

In Europe this species grows upon *L. nummularia*, but I have searched in vain for it upon that host near Cambridge. The specimens from Granville were collected by Mr. A. B. Seymour. The galls are thickly scattered over the leaves, but are of small size. The host-cell is usually spherical and the surrounding cells form rather a thick layer, except at the top of the gall, where there is a depression, at the base of which the host-cell is exposed. The resting spores are large for the genus, as shown by our own as well as European specimens.

9. S. MYOSOTIDIS, Kuehn. var. POTENTILLÆ, Schroeter.

Beit. zur Biol. i, part 1, p. 48.
Bull. Bussey Inst. ii, p. 224, 229.

Spots glandular, deep red, often densely aggregated, galls formed of swollen, externally projecting epidermal cells, resting spores globose, .07–.12mm. in diameter, epispore dark brown.

On leaves and petioles of *Potentilla Canadensis*, L.

Jamaica Plain, Mass. Europe.

An easily recognized but not very common species, which closely resembles the epidermal deformities placed in the old genus *Erineum*. The typical form is found on *Borraginaceæ* in Europe, but our form is precisely that which grows on *P. argentea*, in Europe. To the naked eye the leaves attacked seem to be spotted with shining deep red glands, which are sometimes so abundant as nearly to cover the surface. When young the glands seem to have a white spot in the center, and when old they collapse and become cup-shaped. The glands are nothing but the epidermal cells attacked by the parasite, which causes them to swell into oval or obovate sacks, whose contents become deep red. This

species has, I believe, never been known to produce sori. Our nearest related species is *S. papillatum*, in which the deformity is also confined to the epidermal cells, which swell to a greater size than in the present species and are constantly papillate. *S. papillatum*, however, produces sori of zoösporangia, and belongs to the subgenus *Eusynchytrium*.

What seems to me to be the typical form of the species has recently been found on *Pectocarya linearis*, DC., in Sonora, Mexico, by Mr. C. G. Pringle. The swollen epidermal cells are very numerous, and completely cover the petioles and young stems. When the parasite is immature the cells are yellow, but as the resting spores mature the cells assume the usual deep red color.

10. S. PLURIANNULATUM.

Uredo pluriannulata in Herb. Curtis.
Uromyces pluriannulatus B. & C., Grevillea iii, p. 57.

Spots yellowish brown, galls generally pulvinate or discoidal, composed of several host-cells united into one mass, resting spores numerous (10–50) in a cell, globose or slightly elliptical, .04–.06 mm. in diameter, epispore brown, thick, slightly roughened.

On *Sanicula Marylandica* and *S. Menziesii*, Hook & Arn.

Alabama to Illinois. California.

A very striking species, the development of which should be studied by western botanists. The parasite is abundant on the leaves, petioles and stems. On the leaves it appears in the form of more or less circular, disk-like spots. On the stems the spots are elliptical or lenticular. The disks vary very much in size. The smallest are scarcely raised above the surface of the leaves, and are yellow in color and the surface appears granulated. The larger disks, which are sometimes .40mm. in diameter, have a silvery brown color, and the surface is also granulated. The granulated appearance is owing to the fact that the parasite attacks simultaneously a number of cells lying near one another, which then swell into spherical or elliptical sacks. In the meanwhile the surrounding cells of the leaf which have not been attacked by the parasite multiply rapidly, and the result is a solid disk-like mass in which lie the host-cells, which, seen from above, look like granules. This compound nature of the gall, if we may so term it, is seldom seen in any of our species, but is common in one or two European forms. It is only the very smallest spots that consist of a single host-cell, which is then usually spherical and covered by a thin layer of leaf cells, and I have seen cases where it protruded on both sides of the leaf. The most curious form of the galls is one sometimes found on the petioles and young stems. Here the superficial tissues, as far as one can tell from dried specimens only, grow out at right angles to the stem, so as to form a sort of pedicel, sometimes an eighth of an inch long, and bear at the tip a dark brown head, which contains the host-cells and resting spores. On the larger stems the parasite looks to the naked eye like the sori of a *Puccinia*, owing to the lenticular shape of the spots, which are often surrounded by a fold of the epidermis.

The resting spores are more numerous in a cell than in any other species. I have frequently counted as many as 25, and in some cases the number is un doubtedly greater. The spores are pretty uniform in size, and are spherical or flattened on one side. The epispore is brown, about .004mm. thick, and very brittle, so that it is easily split and separated from the endospore, which has a thin wall, about .0015mm. thick, and yellow oily contents. When the spores are young the epispores closely envelop the endospores, but when mature it is generally the case that the endospore and its contents lie loose in the epispore, thus reminding one of the oospores of *Peronosporeæ*. I have never found sori in this species.

This parasite was first found by Mr. T. M. Peters on *Sanicula* in Alabama, in 1853, and sent to Curtis, who called it *Uredo pluriannulata*. It was first described in Grevillea, iii, p. 57, December, 1874, as *Uromyces pluriannulatus* B. & C. The original specimen of Peters which I have examined has exactly the structure of specimens received from Illinois, collected by Mr. C. A. Hart. I have also, through the kindness of Dr. W. H. Harkness, examined specimens marked *Puccinia Saniculæ*, collected at San Rafael, California, which I can not distinguish from the present species. In all cases the structure is different from that of the *Uredineæ*, and seems to me to be that of *Synchytrium*. The peculiarity of the ripe resting spores, however, shows that the development must be studied before the exact position of the fungus can be decided. In this connection it should be said that there is a *Synchytrium* on *Umbelliferæ*, *S. Bonœrense* Spegazzini, which occurs on *Hydrocotyle bonariensis* in South America, which is known to me only from the description, from which I judge that it is distinct from the present species.

Besides the forms mentioned above, a *Synchytrium* occurs on *Draba Lyallii*, S. Watson, in the Sierra Nevada, but my material is too scanty to warrant a specific description. In my small specimen the leaf is much swollen and irregularly distorted, and a section shows large elliptical resting spores, .13–.18mm. by .08–.10mm., in elliptical host-cells which are closely aggregated and project slightly at the surface of the leaves. It may be that this is only a form of *S. aureum*, known to occur on *Cardamine pratensis*, L., but all the resting spores which I have seen were elliptical, and not globose. With regard to the *Synchytrium* which occurs near Cambridge on *Marrubium vulgare*, on the leaves of which it produces purple spots, I have nothing to add to the account given in my paper in the Bussey Bulletin. Spherical bodies about .06–.075mm in diameter, which are apparently the resting spores of a *Synchytrium*, are contained in epidermal cells which enlarge in the tissue of the leaf but do not protrude beyond the surface, in this respect resembling the form described on *Malcothrix* It would be rash to give a name to a parasite of which so little is known.

In the BOTANICAL GAZETTE, ii. p. 240, a *Synchytrium Jonesii* Peck was described, which grew on *Zauschneria Californica* and *Vicia Americana*. Through the kindness of Mr. Peck I have been able to examine authentic specimens of the parasite on *Vicia* and *Zauschneria*. Sections in both cases show that spores arise from the clavate tips of hyphæ which extend into the leaf, and therefore the species must be excluded from the genus *Synchytrium*. It seems to me that the fungus is nearly related to *Tubercularia persiana* Ditm., and on the leaves of *Vicia* it is in company with an *Æcidium*, as is stated in the original description.

EXPLANATION OF PLATE IV.—Figs. 1–3. *Synchytrium papillatum*, showing (2) a sorus with zoosporangia, and two epidermal galls (1 and 3), one of which is cut open so as to show two resting spores. 500 diam.

4–6. *S. decipiens*, showing section of a gall with a small sorus (4). 400 diam.; 5, a zoosporangium in which zoospores are forming; 6, free zoospores. 600 diam.

7–8. *S. mercurialis* Fuckel. 7, a resting spore with a sorus containing zoosporangia (8) formed by the protruding epispore and its contents. After Woronin.

9. *S. pluriannulatum*. Section through a compound gall showing three host-cells with numerous resting spores. 350 diam.

10. *S. Myosotidis* var. *Potentillæ*. Section through epidermal gall showing a resting spore. 500 diam.

11–12. *S. Holwayi*. Section through two galls showing a resting spore (11) and sorus (12) in which the wall has ruptured and fallen off in the host-cell.

EDITORIAL NOTES

DR. KARL SPEGAZZINI has been appointed professor and director of the botanic garden of Buenos Ayres.

MR. C. G. PRINGLE has left for a season of collecting along the line of the Mexican Central R. R., especially in W. Chihuahua.

DR. JUST has resigned the editorship of the *Botanischer Jahresbericht* at the close of vol. x, and it will be continued by Drs. Koehne of Berlin, and Geyler of Frankfort, conjointly.

PASTEUR, in recent experiments, found that beans and peas did not germinate in soil freed from all bacteria, but what relation the bacteria hold to germination is not known.

THE PAPER on the mite gall of the black walnut, by Miss Lillie J. Martin, which was read before the Amer. Association at Philadelphia, is published in the *Amer. Naturalist* for February, illustrated with three plates. We gave a notice of the paper at p. 155 of the preceding volume.